FIELDIANA

Zoology

Functional Design
of the Air Ventilation Apparatus
and Overland Excursions by Teleosts

Karel F. Liem

A Contribution in Celebration
of the Distinguished Scholarship of Robert F. Inger
on the Occasion of His Sixty-Fifth Birthday

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LANGDON, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63–80. *In* Browman, D. L., and R. A. Schwarz, eds., Spirits, Shamans, and Stars. Mouton Publishers, The Hague, Netherlands.

MURRA, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Functional Design of the Air Ventilation Apparatus and Overland Excursions by Teleosts

Abstract

Comparative functional and structural analyses of the design underlying air ventilation in four phyletic lineages of air-breathing teleosts show that fishes can ventilate either triphasically or quadruphasically. Triphasic fishes create a draft of fresh air progressing from the buccal cavity into the air chamber and out of the opercular cavity. Because such a draft is produced independently of the water, triphasic breathers can abandon water and move overland. Quadruphasic fishes use water to expel the stale gas from the air chamber prior to inhaling fresh air. Because quadruphasic breathing depends on water, quadruphasic fishes are chained to the aquatic habitat and are unable to move overland. Quadruphasic breathing is an evolutionary novelty that has evolved independently in the Anabantoidei and Clariidae. Terrestrial excursions are limited to triphasically breathing fishes.

When air-breathing fishes are subjected to hypoxic and drought conditions in the laboratory as well as in the field, they do not remain in water and even dig elaborate burrows in the substrate. Bottlenecks of intense selection were simulated under laboratory conditions. The frequency of emergence from the water increased significantly when *Monopterus* or *Anabas* were subjected to starvation of increased intra- and interspecific competition for shared prey items in short supply.

Experimental and anatomical evidence is provided to reveal the structural and functional interactions between the feeding and air chambers. The interactions are expressed in networks of interacting constraints. Two kinds of networks are recognized: coupled, in which the chambers have overlapping functions and structures, and decoupled, in which the chambers are functionally sep-arated by valves. This study demonstrates that lineages with decoupled feeding and air chambers possess a greater morphological diversity in the elements associated with the air chambers than lineages in which the chambers are coupled. Thus, the nature of the network of interacting constraints determines morphological diversity.

Based on this broadly comparative experimental study combined with field observations, Inger's theory (1957) that the proximate selective factor in the first terrestrial activities of the prototetrapods was population pressure in a continuously humid climate is strongly favored over the alternative hypothesis, that prototetrapods crawled on land in search of some surviving bodies of water when water was vanishing during extended droughts.

Introduction

Arguing by analogy from the known to the unknown, Inger (1957, p. 374) proposed that "the original selective advantage of an air chamber was to enable fishes to *remain* in the warm water that must have characterized the Upper Devonian." Based on field studies of air-breathing fishes in Borneo, he postulated that the ecological requirements of contemporary fishes indicate that the tetrapods arose in a continuously humid climate because it was the more favorable for invasion of the land. In recent years, considerable physiological evidence has been gathered to demonstrate that numerous freshwater and marine fish species are air-breathers (Bertin, 1958; Gans, 1970; Johansen, 1970; Graham, 1976; Hughes, 1976; Randall et al., 1981). Although the adaptive significance of

air breathing remains uncertain, one hypothesis has been assumed to be correct, or at least has not been questioned: Most air-breathers evolved when environmental factors reduced the suitability of ambient water for aquatic respiration. Laboratory studies have also shown that some species are able to improve their air-breathing capabilities by modulating air-breathing thresholds and frequencies (Randall et al., 1981). It is also known that the operation of bimodal respiratory mechanisms (simultaneously in air and water) in most air-breathing fishes requires intimate contact with ambient water because, even though air breathing meets O_2 requirements, gill ventilation is needed in order to excrete CO_2. The larvae of air-breathing fishes invariably rely on aquatic respiration and often possess special adaptations to cope with hypoxic and anoxic conditions (Liem, 1981). Thus, there are developmental constraints in the respiratory apparatus which limit overland excursions and dictate that air-breathing fishes remain in water.

Recent experimental studies using high-speed cinematography (Ishimatsu & Itazawa, 1981), high speed cineradiography (Peters, 1978; Liem, 1980a; Hellin & Chardon, 1983), and a combination of high-speed cineradiography, electromyography, and pressure recordings (Liem, 1984) have revealed that some air-breathing fishes use water to flush out the gas bubble during air ventilation. Fishes using water to ventilate their air-breathing chamber are called quadruphasic breathers, since four phases can be distinguished in the electromyographic, kinematic, and pressure profiles (Liem, 1985). Since quadruphasic fishes depend on water to ventilate the air chamber, they are chained to the aquatic habitat (Ishimatsu & Itazawa, 1981). Other air-breathing fishes ventilate the air chamber by creating a draft of fresh air progressing from the buccal cavity into the air chamber and out of the opercular cavity. Such a draft of air is created independently from the water. Fishes that ventilate the air chamber by producing a draft are triphasic breathers because the kinematic and electromyographic profiles show three phases (Liem, 1980a). Since triphasic breathers can ventilate the air chamber without the aid of water, they are preadapted to emerge from the water and engage in overland excursions.

Whether an air-breathing fish is capable of invading terrestrial habitats or not seems to depend on the functional design of the respiratory apparatus. In order to assess the general role of the functional design of the respiratory apparatus in the invasion of land habitats, we need a broader experimental data base covering a much wider phylogenetic spectrum of air-breathing fishes than is currently available.

In spite of the great interest in tetrapod origins during the past seven decades (Barrell, 1916), two controversial hypotheses remain untested. The most widely accepted hypothesis suggests that at first terrestrial habits in the earliest tetrapods were confined to migrations from drying pools to those with somewhat more water (e.g., Romer & Parsons, 1977, p. 63; Raff & Kaufman, 1983, p. 193). In sharp contrast, the second hypothesis proposed that terrestrial habits are adopted in a continuously humid climate in the complete absence of stimulation from shrinkage of water volume (Inger, 1957).

The goals of this paper are threefold: (1) to provide an expanded empirical data base on air-breathing fish species belonging to various phyletic lineages. Such a comparative approach forms a foundation for understanding the importance of historical factors in canalizing mechanisms underlying air ventilation and in limiting adaptive potentials for terrestrial invasions; (2) to examine experimentally the various factors triggering the emergence of air-breathing fishes from the water under laboratory conditions and to review the evidence from observations in nature; and (3) to evaluate the two hypotheses on the origins of tetrapods (continuously humid vs. dry climatic conditions) in light of the new empirical data base.

Materials and Methods

The fishes used in this study were imported from Thailand and Malaysia. They were fed on live goldfish (*Carassius auratus*), guppies (*Poecilia reticulata*), frozen smelt (*Osmerus*), Tetramin fish food, *Tubifex,* and frozen brine shrimp (*Gammarus*).

The following species have been studied:

Monopterus albus, 49 specimens (21–43 cm in total length) (Synbranchiformes); *Luciocephalus pulcher,* 3 specimens (11–14 cm in total length) (Luciocephalidae, Anabantoidei); *Anabas testudineus,* 22 specimens (7–12 cm in total length) (Anabantidae, Anabantoidei); *Osphronemus goramy,* 4 specimens (13–17 cm in total length) (Osphronemidae, Anabantoidei); *Betta splendens,* 22 specimens (5–8 cm in total length) (Belontiidae, Anabantoidei); *Macropodus opercularis,* 21 spec-
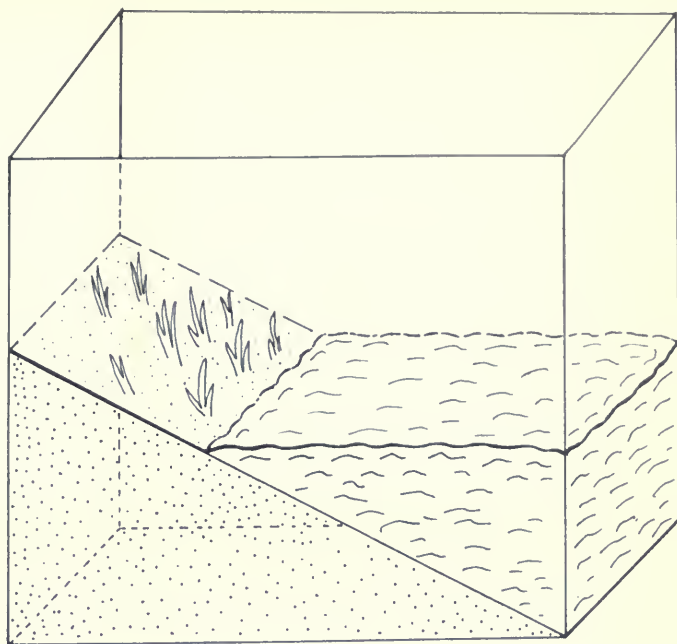
Fig. 1. Diagram of experimental tank in which observations were made on frequency of emergences from the water by various air-breathing fishes in response to deoxygenation of water, a rise of environmental temperature, starvation, increase in population density of conspecifics, and mixing with other species competing for common food resources.

imens (7–11 cm in total length) (Belontiidae, Anabantoidei); *Trichogaster trichopterus,* 29 specimens (7–9 cm in total length) (Belontiidae, Anabantoidei); *Clarias batrachus,* 2 specimens (14–15 cm in total length) (Clariidae, Siluroidei).

In order to visualize the location and movements of the gas bubble, high-speed cineradiographic films were made. Such a visualization of a rapidly moving gas bubble is important in determining the precise mode of ventilation and how it relates to other functions such as feeding and coughing. Electromyography synchronized with pressure recordings enables us to understand the physiological origin of air ventilation (Liem, 1980a) and its possible evolutionary origin in a comparative analysis. With the pressure recordings we can determine the mechanism of air ventilation very precisely. Cineradiographic, electromyographic, and pressure analyses were performed on key species of major phylogenetic assemblages in order to decipher convergent evolution and the occurrence of adaptive radiation in hypoxic environments.

High-speed x-ray cine films were produced by a Siemens radiographic unit with a Sirecon image intensifier and an Eclair GV-16 camera at 150 frames sec⁻¹. Kodak Plus-X Reversal film was exposed at 300 mA and 49 kV. The fish was filmed in a narrow chamber with very thin plastic walls to minimize the loss of contrast. Films were taken from lateral as well as dorsoventral views and were analyzed with a Lafayette variable speed projector.

The pressures developed in buccal, opercular, and suprabranchial chambers were recorded by the introduction of flexible polyethylene cannulae (I.D., 0.86 mm; O.D., 1.52 mm). The buccal cavity was reached by a hole drilled through the skull roof and parasphenoid from a point midway between the snout and eyes, and passed through the roof of the mouth. The suprabranchial chamber was reached by a hole drilled in the pterotic bone just posterior to the posterior head of the hyomandibula. Access to the opercular cavity was gained by a hole through the anterior surface of the cleithrum at the level of the pectoral fin. Pressures were recorded with Statham P23 Gb and P23 Db pressure transducers, which were dampened (Lauder, 1980) by filling them with a mixture of 45% water and 55% glycerine. Great care was taken to ensure that no air was present in the fluid-filled cannulae, syringes, and pressure transducers. After each air breath, the cannula was flushed. Signals from the pressure transducers were amplified by Gould Carrier Amplifiers and recorded on a Bell and Howell 4020 A FM 14-channel tape recorder and a Gould-Brush 260 pen recorder.

Electromyograms were obtained with bipolar electrodes (Evenohm S) using the method of Bas-

majian and Stecko (1962). Pairs of wires, cleaned and hooked at the tip, were threaded through a 25-gauge hypodermic needle. This needle was inserted through the skin to the desired site and was then withdrawn, leaving the electrodes hooked into the muscles. Electromyographic signals were amplified with Grass 511J preamplifiers, recorded on the Bell and Howell tape recorder, and displayed on the Gould-Brush 260 pen recorder.

Laboratory experiments on various factors triggering emergence from water by air-breathing fishes were conducted in a large rectangular aquarium. The aquarium was filled with water 40 cm deep, and at one end a sloping sand beach measuring approximately 50 cm long and 50 cm wide was made (fig. 1). Short vegetation was planted on the beach. A tent was placed around the aquarium; within the tent, illumination and temperature could be controlled. The behavior of the fish could be observed through several small windows in the tent. Observations were made by two persons on opposite sides of the tent. The fish were acclimated for 14 days before the various observations were made. The major objective of these procedures was to determine how water levels, oxygen and temperature levels of the water, starvation, increase in population density of conspecifics, and that of other species competing for common food resources affect the frequency of emergences from water in various air-breathing fishes.

Fish were observed continuously over a 24-hour period by six pairs of students. The score represents the average of individuals on the beach of counts made at half-hour intervals over the 24-hour period. No attempt was made to identify individuals. When a particular fish moved back and forth from the water to the beach, it was only recorded if it happened to be out of water on the hour or on the half-hour when the count was made

by the two observers. No corrections were made for repeated and short emergences. During the observations it was noted that once a fish left water, it often returned to it. Thus the data presented do not deal with the total duration of emergence of a particular individual fish. The goal is to record the behavior of the entire population in response to an environmental perturbation. The details of the various manipulations will be discussed in subsequent chapters of this paper.

Water-Dependent Ventilatory Mechanisms: Quadruphasic Species

Quadruphasic fishes expel the gas bladder by flushing it out with water.

Pattern

Most members of the Anabantoidei have air ventilation mechanisms that are obligatorily dependent on water (Peters, 1978; Liem, 1980a). The quadruphasic pattern of the highly specialized species *Luciocephalus pulcher* is representative of most Anabantoidei examined (Liem, 1980a, 1985), but differs in that air is held not only in the suprabranchial chambers but also in the pharyngeal area.

Cineradiographic recordings (fig. 2) show that the air-breathing cycle in *Luciocephalus* begins with the complete explusion of the air from the suprabranchial air chamber (fig. 2A). The stepwise replacement of air by water can be followed in the successive frames of the cineradiographic film. First the air of the posterodorsal compartment of the suprabranchial chamber is forced forward and

FIG. 2. Representative prints from an x-ray cine film at 100 frames/second during air ventilation in *Luciocephalus pulcher* (standard length 12 cm). Film was taken in lateral projection. **A,** The fish approaches the water surface with its suprabranchial cavity (s) filled with air. Note that the buccopharyngeal cavity (b) is devoid of air. The fish has its snout protruded from the water. Anterior chamber of gas bladder (g) and parasphenoid (p) are also shown. **B,** Exhalation has started. The air has been replaced by water in the posterodorsal compartment of the suprabranchial cavity. The forward flush of the air bubble is clearly discernible, as most of the air from the suprabranchial cavity is now occupying the buccopharyngeal cavity, from which it leaves the fish through the opened mouth protruding from the surface of the water. **C,** Exhalation has been completed. All air has been flushed out from the suprabranchial and buccopharyngeal cavities. The fish remains at the surface with its mouth momentarily closed but still protruded from the water surface. **D,** Inhalation has started as the fish is sucking fresh air into its buccopharyngeal cavity, which distends and becomes fully filled with air in less than 10 msec. At this stage air is confined to the buccopharyngeal cavity. **E,** The fish sinks below the surface of the water, and air from the buccopharyngeal cavity is being compressed into the suprabranchial chamber, which can be seen being filled with air. **F,** The suprabranchial chamber is now completely filled with air, and the ventilation cycle has been completed. Duration of ventilation cycle is 210 msec.
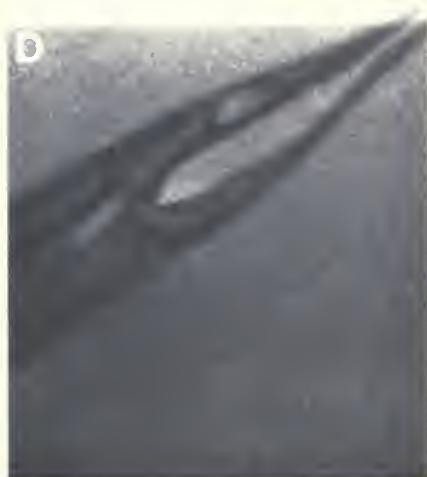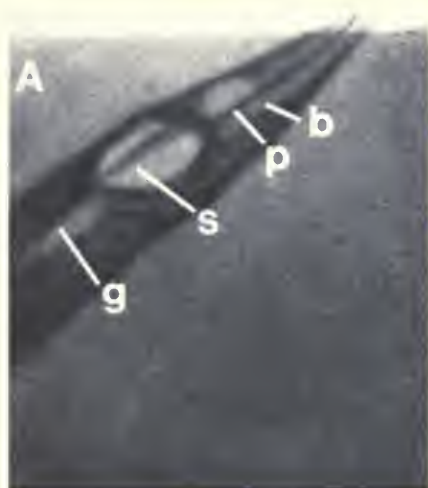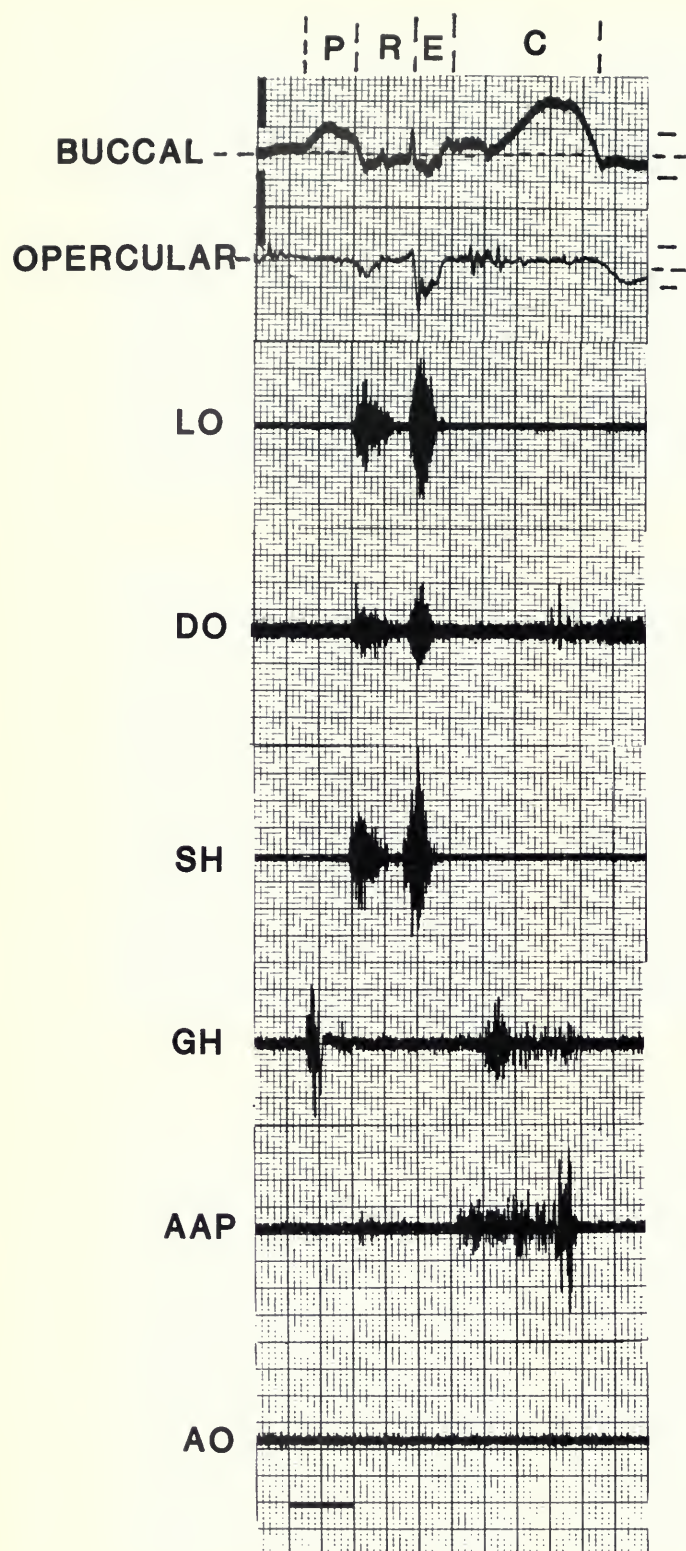
FIG. 3. Pressure waveforms of the buccal and opercular cavities, together with electromyograms of the head muscles of *Osphronemus goramy* during air ventilation. Electromyographic and pressure profiles are composites of recordings selected from 19 sequences. Pressure scale is 50 cm H_2O; time scale is 50 msec. Four phases are recognized in this representative quadruphasic mode of ventilation: preparatory (P), reversal (R), expansive (E), and compressive (C). AAP = adductor arcus palatini muscle; AO = adductor operculi muscle; DO = dilatator operculi muscle; GH = geniohyoideus muscle; LO = levator operculi muscle; and SH = sternohyoideus muscle.

downward by the advancing reversed flow of water (fig. 2B). As the water continues to flow anteriorly, all air is expelled through the mouth (fig. 2C). Inhalation starts with the filling of the buccal cavity with air (fig. 2D) by a sudden expansion of the buccal cavity. At this time, the opened mouth protrudes from the water surface. The fish then closes its mouth and returns into the water, compressing the air from the buccal into the suprabranchial air chamber (fig. 2E–F).

Functional Basis

The anatomy of the suprabranchial air chamber and the musculoskeletal aspects of the Anabantoidei have been treated exhaustively elsewhere (Liem, 1963, 1967a,b, 1980a; Peters, 1978) and will not be repeated here. Instead I will focus on the pressure changes and the sequences of muscle actions during air ventilation, which have not been analyzed previously.

Pressures in the buccal and suprabranchial cavities were recorded synchronously with electromyograms of six key respiratory muscles (fig. 3) in *Osphronemus goramy*. The data indicate that the air ventilatory cycle is quadruphasic and representative of all the Anabantoidei studied. The cycle begins with a preparatory phase during which the buccal pressure rises because of action of the geniohyoideus muscle. This compressive action maximizes the pressure drop, which occurs in the subsequent reversal phase. Action of the sternohyoideus muscle brings about a significant expansion of the buccal cavity, causing a large decrease (25–35 mm H_2O) in the buccal pressure. At the same time the dilatator operculi is active, creating a drop (20–30 mm H_2O below ambient pressure) in the opercular cavity, which is also held open. As a result, water is drawn from the exterior through the opened opercular valve into the opercular cavity. Such a flow is made possible because of the gradient from the ambient pressure of the exterior to the lower pressure in the opercular cavity, to the even lower pressures of the suprabranchial and buccal cavities. The reversed water flow proceeds via the suprabranchial air chamber into the buccal cavity, which has generated the lowest pressure. This reversed flow of water drives the gas from the suprabranchial chamber into the buccal cavity and forward out of the mouth, which is opened by action of the levator operculi muscle (fig. 3). Thus the reversed water flow constitutes the principal driving force to flush out the gas bubble from

the air chamber. Exhalation is obligatorily linked to water. Without water, the fish is unable to force the gas from its suprabranchial air chamber. In the third phase, the expansive phase, inhalation begins with sharp pressure drops in both the buccal and opercular cavities by combined actions of the sternohyoideus and dilatator operculi muscles, causing air to be drawn in through the mouth, which is opened by the levator operculi muscle (fig. 3). The fresh air in the buccal cavity is then compressed by combined actions of the geniohyoideus and adductor arcus palatini muscles. During this extended compressive phase (fig. 3), the pressure in the buccal cavity rises as high as 50 cm H_2O above ambient. Inhalation by expanding and compressing the buccal cavity does not require any water and proceeds normally in the absence of water.

Laboratory and Field Observations of Quadruphasic Species

The effects of oxygen depletion and water temperature manipulations on the behavior of the fish were analyzed under controlled laboratory experiments. Laboratory observations were made on *Betta splendens, Macropodus opercularis, Osphronemus goramy, Helostoma temmincki,* and *Trichogaster trichopterus,* all of which ventilate air by the water-dependent quadruphasic mechanism. The fishes were exposed to water containing pO_2 of 5, 10, and 150 torr over 24-hour periods. None of the fishes would emerge from the water under these various concentrations of oxygen. Thus low oxygen tensions do not trigger overland excursions (table 1). Likewise elevated temperatures of 34°C. maintained over 24-hour periods have no significant effects on the behavior of these fishes.

A series of experiments were executed to determine the effects of food supply, population density, and interspecific competition on voluntary emergence from water by the above-mentioned quadruphasic species. Sharply reduced food resources over 14 days while other environmental parameters were carefully kept at the control level did not elicit voluntary emergences from water (table 1). A doubling of the population density by adding 10 conspecifics of the same size range failed to induce terrestrial sojourns. Likewise, the addition of equal numbers of different species, which are potential competitors for food resources and shelter, did not result in a single emergence from

TABLE 1. Number of emergences (± standard error) over 24-hour periods under various environmental perturbations.

	No. of emergences by various species (N = 10)				
Perturbation	Monopterus	Anabas	Betta	Macropodus	Tricho-gaster
Control	2.1 ± 0.01	1.09 ± 0.03	0	0	0
p [O₂] 5 torr	2.2 ± 0.02	1.02 ± 0.01	0	0	0
Starvation for 14 days	8.1 ± 0.31*	7.5 ± 0.17*	0	0	0
Raised temperature, 34°C.	3.1 ± 0.09	0.5 ± 0.03	0	0	0
Addition of 10 Monopterus	19.3 ± 0.08*	NA	NA	NA	NA
Addition of 10 Nandus	9.7 ± 0.09*	9.4 ± 0.11*	NA	NA	NA
Addition of 10 Carassius	2.1 ± 0.09	2.1 ± 0.13	0	0	0
Addition of 10 Anabas	NA	17.9 ± 0.12*	NA	NA	NA
Addition of 10 Betta	NA	NA	0	0	0
Addition of 10 Macropodus	NA	7.8 ± 0.13*	0	0	0
Addition of 10 Trichogaster	NA	7.3 ± 0.09*	0	0	0

NA = Not applicable.
* 99% confidence interval non-overlapping with control.

the water in the five species studied over the 24-hour periods of observation (table 1). These laboratory manipulations indicate that quadruphasic species do not engage in any terrestrial excursions even under the most stressful environmental conditions. The responses of the species to these perturbations are restricted to changes in aquatic behavior primarily involving the modulation of air-breathing frequencies and the shifting of their vertical positions in the aquatic habitat.

When quadruphasic species are taken out of the water under laboratory conditions, the fish undergo respiratory stress. Each of the observed species attempts to gulp air by uncoordinated movements of the buccal and opercular elements, which are simultaneously flared and compressed. Individuals of each species continue to struggle, executing vigorous movements of the operculum, hyoid, sidewalls of the mouth cavity, and jaw for varying periods (30–210 minutes) before they succumb. Even though neither electromyographic nor pressure recordings were possible because of the vio-

lent movements of the fish, it appears that these species will continue to ventilate their aerial chambers by the quadruphasic mode while out of water. Consequently they are unable to exhale the gas fully from their air chambers, resulting in respiratory stress.

My field observations on Betta, Macropodus, Osphronemus, and Trichogaster in Western Java (Indonesia) indicate that these taxa do not engage in terrestrial excursions whether the ponds are drying out during the dry season or after heavy rains. Inger (1955) has observed that in Borneo (Kalimantan), Betta is frequently found above waterfalls as high as 5 m, and suggests that Betta moves overland to bypass waterfalls of considerable height. However, I have not seen any other reports confirming Betta's abilities to engage in substantial terrestrial sojourns. Because Betta depends on the quadruphasic mode of air ventilation, which makes it obligatorily dependent on water, it seems unlikely that it can emerge from the water for any length of time. Thus, with the

Opposite Page:

FIG. 4. Representative prints from an x-ray cine film at 100 frames/second during air ventilation in *Monopterus albus* (standard length 33 cm). Film was taken in lateral projection. **A,** The fish has air in its buccopharyngeal and opercular cavities and esophagus. The vertebral column (v), pectoral girdle (p), hyoid (h), mandible (m), and neurocranium (n) are discernible and in the typical positions when the cavities are extended and filled with air. **B,** Exhalation has started. With the mouth closed, the hyoid and pectoral girdle are changing from the vertical position (as seen in **A**) into more horizontal orientations as air is forced out. **C,** Exhalation proceeds as air bubbles continue to leave the fish, especially from the external gill slit. The multiple air bubbles can be seen as turbulence around the fish. **D,** Exhalation is very near completion, as most of the air has been expelled. **E,** Inhalation has started and air has entered in the buccopharyngeal cavity. **F,** Inhalation is completed, as fresh air is now occupying not only the buccopharyngeal cavity, but also the opercular cavities and esophagus. The duration of the ventilation cycle is 550 msec.
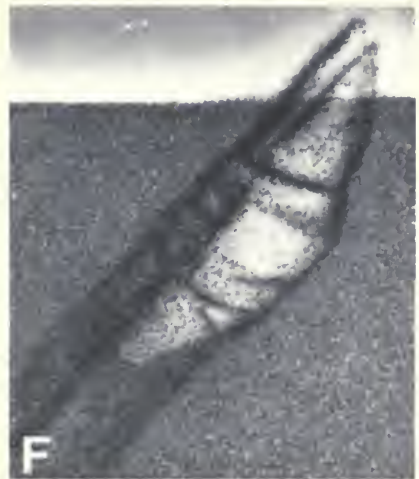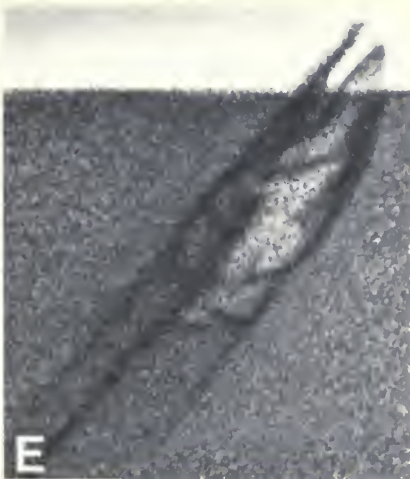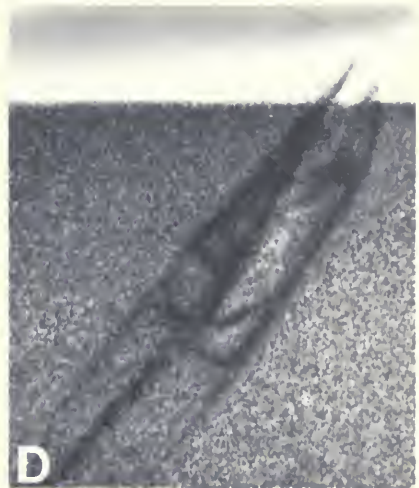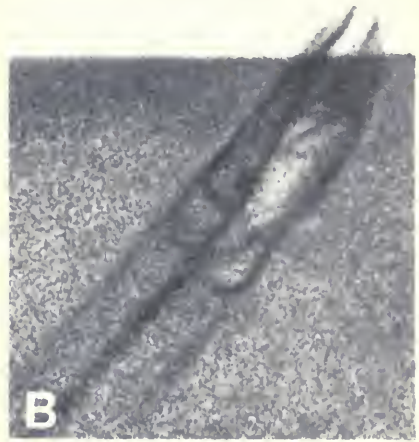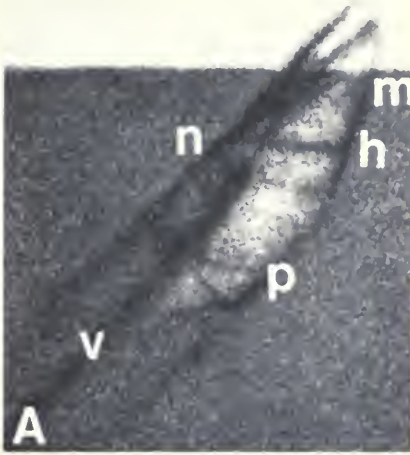
possible exception of *Betta,* quadruphasic species are purely aquatic throughout their life history cycle, using their air-breathing capabilities to remain and even thrive in warm, stagnant waters deficient in oxygen.

Water-Independent Ventilatory Mechanism: Triphasic Species

Triphasic species ventilate their air chambers by creating a draft.

Pattern

Several members of the Anabantoidei (Peters, 1978; Liem, 1980a), *Clarias* (Donnelly, 1973; Hellin & Chardon, 1983), and most Synbranchiformes exhibit varying triphasic patterns of air ventilation.

In the anabantoid *Anabas* and *Helostoma,* the triphasic pattern has been described (Peters, 1978; Liem, 1980a, 1985): A draft of air is created by gulping fresh air at the surface. Once the mouth is filled with air, the fresh air is forced into the suprabranchial chamber, replacing the stale air, which is forced out of the suprabranchial chamber into the opercular cavity. Because the opercular cavity is compressed while the opercular valve is opened, the stale air escapes from under the gill cover. Thus, during the entire ventilatory cycle, the suprabranchial chamber remains filled with air.

In *Clarias lazera, C. batrachus,* and *C. gariepinus,* two modes of ventilation occur, depending on the water level. When water levels are adequate, *Clarias* exhales first by releasing stale air through the opercular openings just before the mouth reaches the surface to take in fresh air (Donnelly, 1973; Hellin & Chardon, 1983). However, when *Clarias* is either in very shallow water or out of water, it ventilates its air chamber by the triphasic pattern. The fish raises its head and enlarges its mouth cavity, thereby sucking in air through the opened mouth. Once the mouth cavity is filled, the mouth is closed and the head depressed. The buccal cavity is compressed, forcing the fresh air into the suprabranchial chamber, replacing the stale air, which escapes into the opercular cavity. The opercular cavity is then compressed to force the stale air from underneath the gill covers. The air bubbles extrude through the opercular openings, creating distinct noises when the fish is in mud (Donnelly, 1973).

Synbranchiform fishes also exhibit two modes of air ventilation (Liem, 1980a). All synbranchiform fishes exhale prior to inhalation. Exhalation can proceed either passively by the use of hydrostatic pressure and air buoyancy itself or actively by muscular effort. During passive exhalation the fish surfaces and protrudes its snout out of the water and then opens its mouth slightly, allowing air to escape from the mouth (Lüling, 1958). Active exhalation can proceed while the fish is on the bottom, in the water column, or at the surface; it is independent of the body position and gas is forced out of the mouth, although some often escapes from the single median gill opening. During exhalation, the hyoid and consequently the floor of the buccopharynx is raised. During exhalation, the hyoid rami are rotated forward and upward, thereby raising the floor of the mouth (fig. 4). At the same time lateral compression of the buccopharyngeal cavity also occurs because the angle between the two hyoid rami is greatly reduced (fig. 5). These compressive movements force the gas out of both the mouth and median external gill slit. After exhalation the fish ordinarily inhales by

Opposite Page:

FIG. 5.   Representative prints from an x-ray cine film at 100 frames/second during air ventilation in *Monopterus albus* (standard length 43 cm). Film was taken in dorsoventral projection. **A,** With the air-filled buccopharyngeal and opercular cavities fully distended, the hyoid (h) and pectoral girdle (p) are abducted, showing a large angle between the left and right halves. Air extends far posteriorly into the esophagus. The opercular cavities surrounding the gills are also completely filled with air. The vertebral column (v), neurocranium (n), and mandible (m) are clearly projected. **B,** Exhalation has started. The angles between the right and left halves of the hyoid apparatus and pectoral girdle are being reduced to compress the air. **C,** Compression is proceeding, as the remaining air is forced out from the opercular cavities by continued reduction of the angle between the left and right halves of the hyoid and pectoral girdle. **D,** Exhalation is now completed; there is no residual air and the gill arches can be seen. **E,** Inhalation has begun, as fresh air is drawn in by the sudden extension of the buccopharyngeal cavity as the angles between the hyoid and pectoral girdle halves increase. **F,** The ventilation cycle has been completed, as all cavities are refilled with air, and the orientation of the pectoral girdle and hyoid is restored as in **A.** The duration of the ventilation cycle is 600 msec.
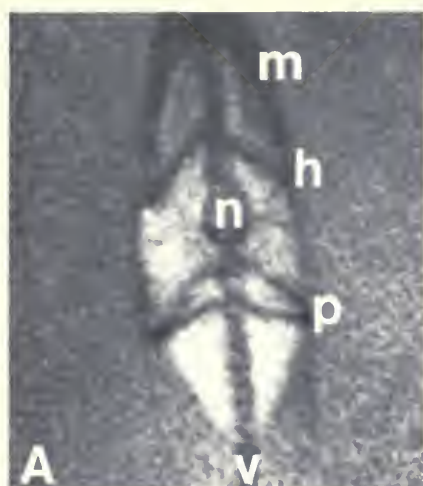
surfacing, protruding the snout slightly out of the water, and lowering the hyoid rami and therefore the floor of the mouth. Air is sucked in rapidly by the sudden expansion of the buccopharyngeal and opercular cavities. The expansion is brought about by lowering the hyoid rami in such a way that their long axes make 90° angles with the neurocranial base (fig. 4), causing the floor of the mouth to drop significantly. At the same time, lateral expansion of the buccopharyngeal cavity is accomplished by an increase in the angle between the hyoid rami, as can be seen from dorsoventral projections of the cineradiographic images (fig. 5). When inhalation is completed, the buccopharyngeal and opercular cavities are completely filled with air. Thus the epithelial lining, the entire buccopharyngeal and opercular cavities, and the gill filaments are exposed to air (figs. 4–5).

When the level of the water is lowered, the fish continues to ventilate air by the active exhalation mode. However, after it has emerged from the water for 20–45 minutes, *Monopterus* invariably opens its mouth widely and intermittently performs ventilatory movements by alternating adduction and abduction movements of the lower jaw, hyoid, and opercular apparatus. Similar observations have been made on *Synbranchus* by Johansen (1966).

All modes of air ventilation in the synbranchiform fishes are independent of water. Stale air is expelled by direct compression, and new air is sucked in by a muscularly effected expansion producing a sudden low pressure in the respiratory chambers.

Functional Anatomical Basis

Because the functional patterns in the three taxa are very different, they will be described individually.

ANABANTOIDEI—*Anabas* invariably ventilates in the triphasic mode, while *Ctenopoma* and *Helostoma* are capable of ventilating either triphasically or quadruphasically. The triphasic pattern begins with a preparatory phase (fig. 6) when the buccal pressure shows a sharp rise, coincident with activity in the geniohyoideus and adductor arcus palatini muscles. The preparatory phase is immediately followed by the expansive phase, during which there is a sudden drop in buccal pressure coincident with high amplitude activity in the levator operculi and sternohyoideus muscles. Both the preparatory and expansive phases are of short du-

ration and are followed by the prolonged compressive phase (fig. 6C) which is characterized by activity in the geniohyoideus and adductor arcus palatini muscles, causing a very sharp rise in the buccal pressure. Near the end of the compressive phase, the adductor operculi becomes active and, as a result, there is a pronounced increase in opercular cavity pressure, which is followed by an action of the dilatator operculi. During the preparatory phase, the volume of the buccal cavity is minimized in order to maximize the subsequent expansive phase during which air is sucked in, since the head is lifted up and the snout protrudes from the water surface. By starting out from the smallest possible volume, suction can be maximized (Osse, 1969). Once the buccal cavity is filled with air, it is strongly compressed by the action of the geniohyoideus and adductor arcus palatini muscles, thereby forcing the fresh air into the suprabranchial chamber. The stale air escapes into the opercular cavity and is forced out from underneath the operculum by the action of the adductor operculi muscle. As a result, during the triphasic mode of air ventilation, the suprabranchial chamber remains filled with air throughout the ventilatory cycle (Liem, 1980a, 1985). Furthermore, the triphasic mode of ventilation is independent of water, since air is moved from one chamber to another by the creation of a pressure gradient resulting in a "draft." Water currents do not play a role in the shifting of air bubbles from one cavity to the other.

CLARIIDAE—Clariid fishes exhibit two distinct modes of ventilation (Donnelly, 1973; Hellin & Chardon, 1983; pers. obs.). Preliminary studies on *Clarias batrachus* indicate that the triphasic pattern of ventilation is employed by the fish whenever water levels become inadequate for quadruphasic ventilation (fig. 7). *Clarias* starts with a preparatory phase, and the expansive phase is brought about by actions of the sternohyoideus muscles, which results in a sudden expansion of the buccal cavity, opening of the mouth, and drop in buccal pressure. Once air has been sucked in, the geniohyoideus shows prolonged activity. The fresh air is compressed in the buccal cavity and forced into the suprabranchial cavity. Stale air is forced into the opercular cavity, from which it escapes by action of the adductor operculi muscle.

SYNBRANCHIFORMES—Among air-breathing lineages, the Synbranchiformes exhibit an amazingly complete evolutionary spectrum, starting from the purely aquatic-breathing, primitive *Macrotrema caligans* to such intermediate, facultatively air-
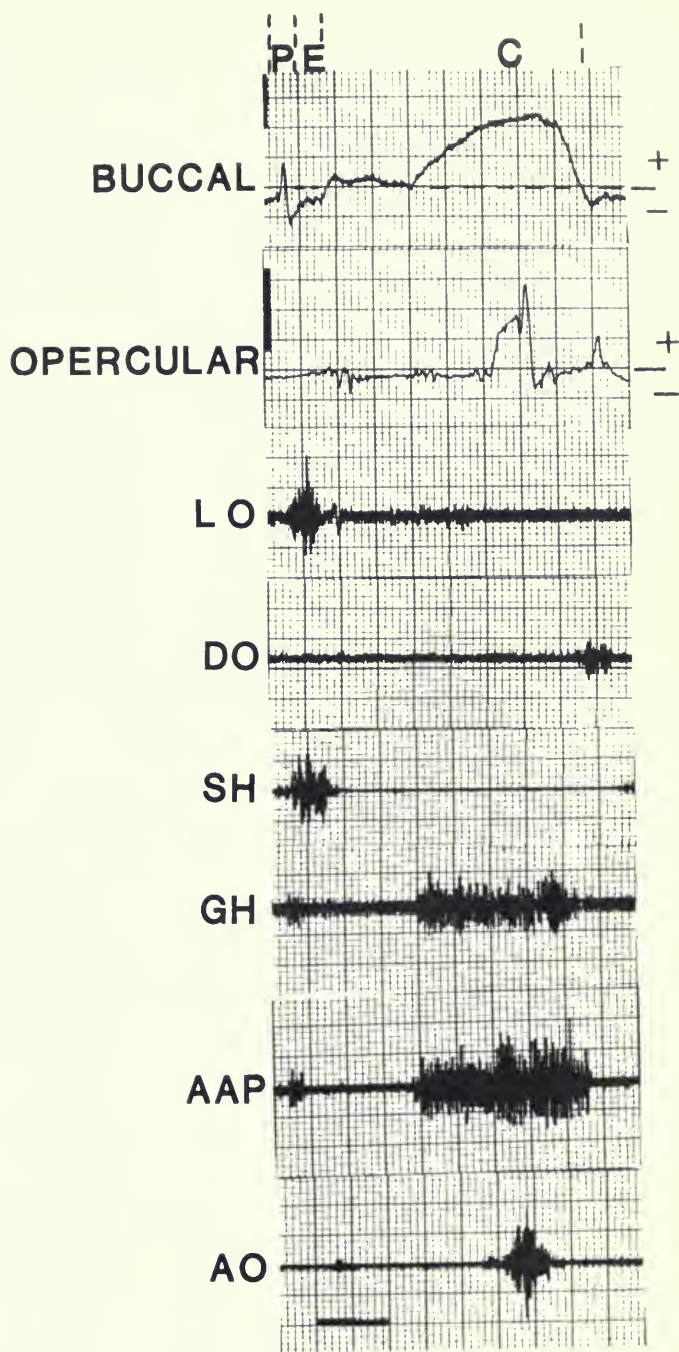
Fig. 6. Pressure waveforms of the buccal and opercular cavities, together with electromyograms of principal cephalic muscles of *Anabas testudineus* during air ventilation. Electromyographic and pressure profiles are composites of recordings selected from 12 sequences. Pressure scale is 50 cm H_2O; time scale is 50 msec. Three phases are recognized in this representative triphasic mode of ventilation: preparatory (P), expansive (E), and compressive (C). AAP = adductor arcus palatini muscle; AO = adductor operculi muscle; DO = dilatator operculi muscle; GH = geniohyoideus anterior muscle; LO = levator operculi muscle; and SH = sternohyoideus muscle.

breathing forms as *Ophisternon* and *Synbranchus*, and culminating in the specialized obligatorily air-breathing species of *Monopterus*.

Structurally, the respiratory apparatus of *Macrotrema* represents the most primitive state among synbranchiforms. The gills resemble those of generalized percomorphs. The holobranch (fig. 8A) is composed of two symmetrically arranged primary gill filaments with well-developed secondary gill filaments. Each primary filament is supported by
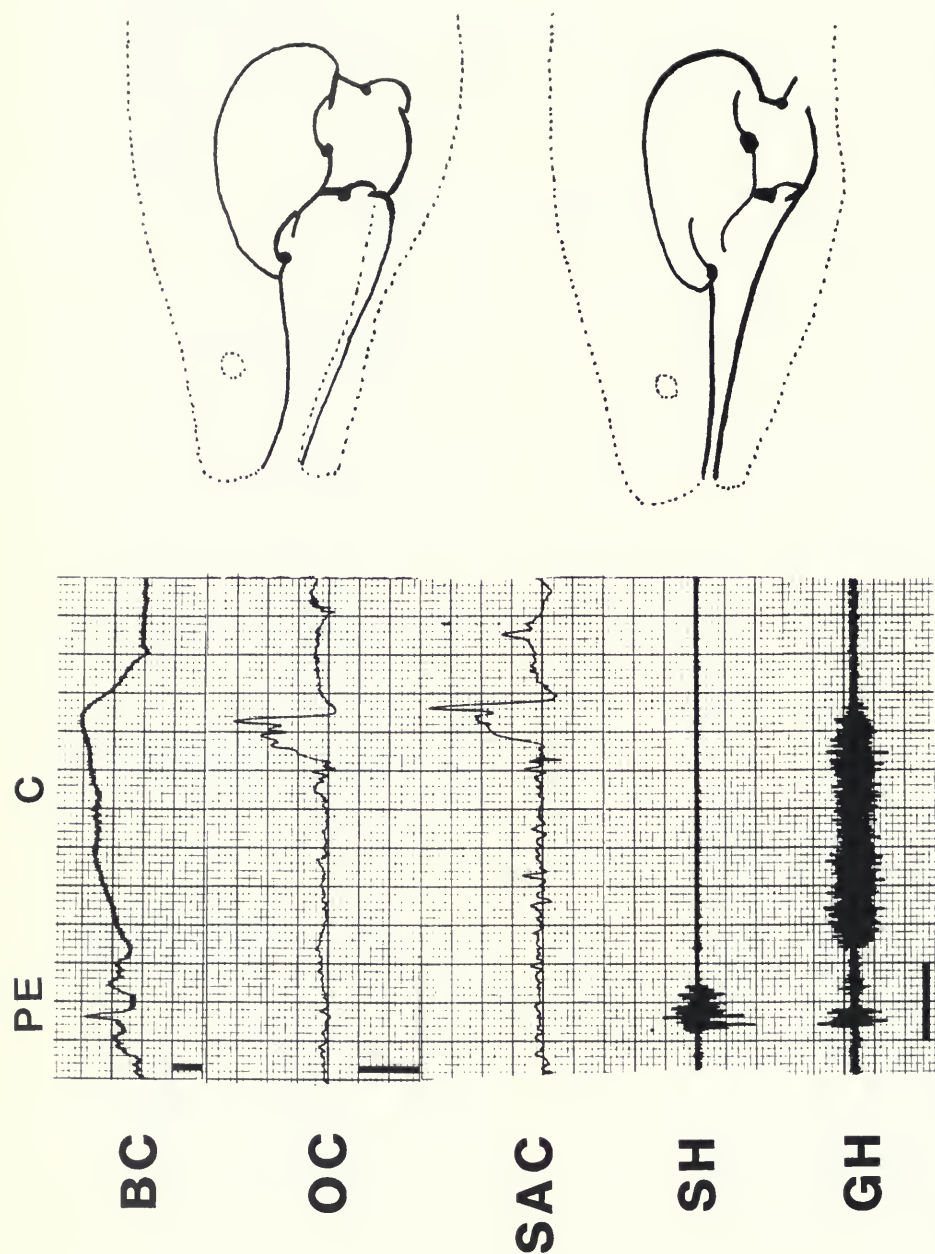
Fig. 7. Pressure waveforms of the buccal, suprabranchial, and opercular cavities, together with electromyograms, in *Clarias batrachus* during triphasic air ventilation. **Right (top)**, Diagram of buccal, suprabranchial, and opercular cavities in expansive phase, during which all valves are closed while air is sucked in through the open mouth into the expanding buccal cavity. **Right (bottom)**, The form of the three cavities and opened valves are depicted during the compressive phase. Pressure scale is 50 cm H_2O; time scale is 50 msec. **Left**, Three phases are recognized: preparatory (P), expansive (E), and compressive (C). BC = buccal cavity; GH = geniohyoideus; OC = opercular cavity; SAC = suprabranchial air chamber; and SH = sternohyoideus.
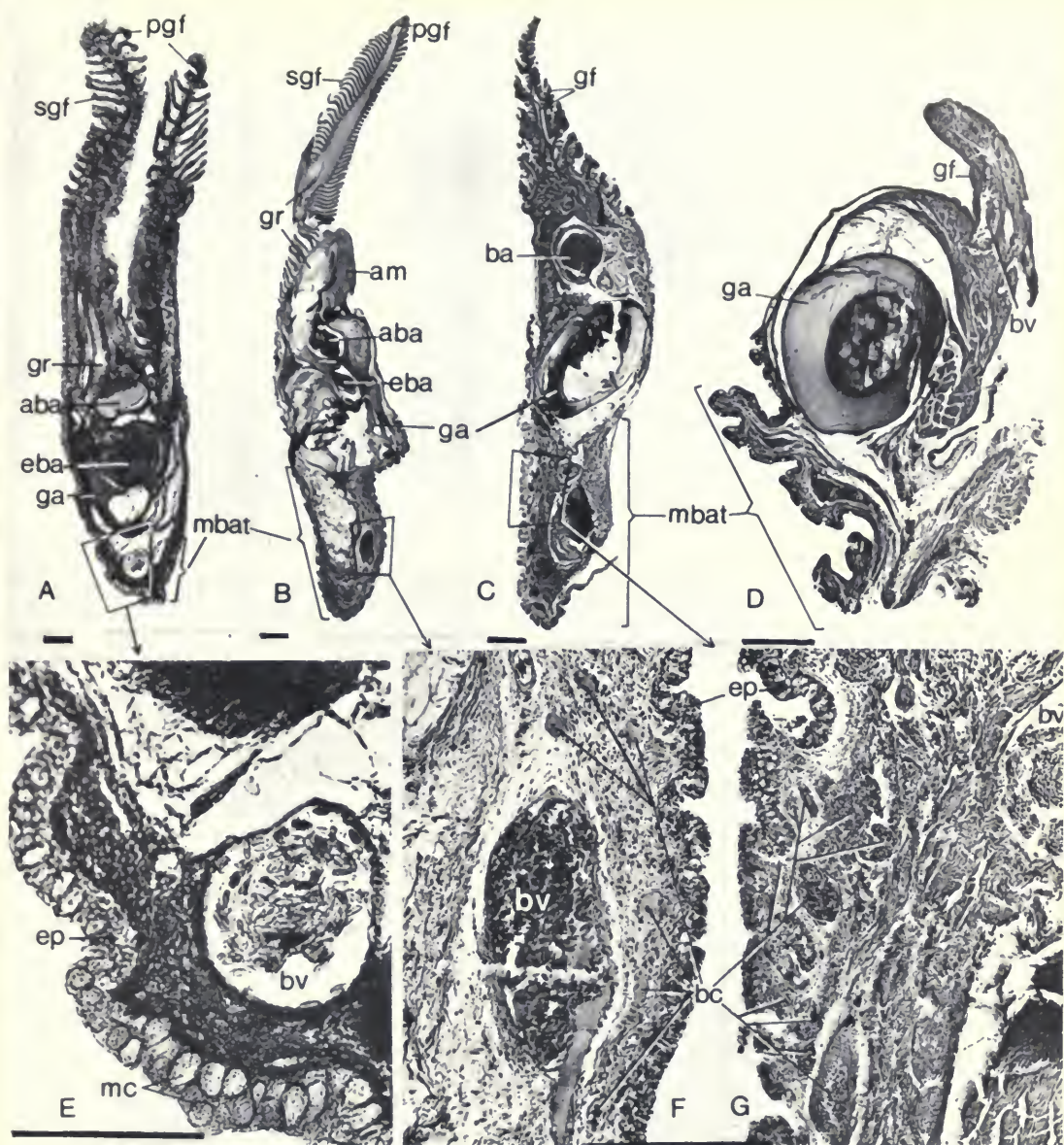
FIG. 8. **Top,** Cross section of holobranch of fourth gill arch: **A,** *Macrotrema caligans*; **B,** *Synbranchus marmoratus*; **C,** *Monopterus albus*; and **D,** *M. boueti*. Note progressive reduction of the primary gill filaments (pgf, gf) and compensating proliferation of the respiratory mucosa lining the buccal aspects of the branchial arches (mbat). Afferent branchial artery (aba), adductor branchialis muscle (am), branchial artery (ba), blood vessel (bv), efferent branchial artery (eba), gill arch element (ga), gill ray (gr), and secondary gill filament (sgf) are also shown. **Bottom,** Higher magnification of the respiratory mucosa of the branchial arches: **E,** *Macrotrema*; **F,** *Monopterus albus*; and **G,** *M. boueti*. Blood capillary (bc), blood vessel (bv), epithelium (ep), and mucous cell (mc) are also shown. Hematoxylin and eosin stain; scale is 0.2 mm.

a gill ray. The mucosa covering both the buccal surface of the gill arch (fig. 8A) and the pharynx is unmodified but is only moderately vascular (fig. 8E).

In the facultative air-breathers, the gills have become very specialized. It has been established experimentally that the gills in *Synbranchus* are functional during air breathing (Johansen, 1966;

FIG. 9. Segment of fourth gill arch and associated gill filaments of *Synbranchus marmoratus* to show the linear arrangement of the holobranchs. Each pair of arrows indicates a pair of demibranchs, each pair of which constitutes one holobranch. Mucosa of branchial arch (mbat) is also shown. Scale is 0.4 mm.

Lüling, 1958). The gills are exposed to air because during breath holding the opercular cavities surrounding the gills are seen to be filled with air on cineradiographs (Liem, 1980a; figs. 4–5). The holobranchs of *Synbranchus* (fig. 9) are arranged linearly but asymmetrically on the gill arch. This asymmetrical linear arrangement in *Synbranchus* is unique and may represent an effective mechanical solution preventing gills or adjacent arches from sticking together when the gill cavity is filled with air. Furthermore, the gill rays are hypertrophied, extending to the very tip of each primary filament and are arranged in a spiral configuration (fig. 8B), giving the gill filament the support necessary to prevent their collapsing when the gills are exposed to air. The mucosa covering the buccal aspect of the branchial arch (fig. 8B) is hypertrophied and greatly vascularized (fig. 8F). Gas exchange is therefore not restricted to the secondary gill filaments but can also take place in the mucosa as well. In *Synbranchus* the entire buccopharyngeal epithelium is provided with numerous blood capillaries (fig. 8B) and plays an important role in gas exchange while the fish is air-breathing (Johansen, 1966). In the most specialized forms, such as *Monopterus albus* (fig. 8C) and *M. boueti* (fig. 8D), the gill filaments become greatly reduced while the mucosa lining the remainder of the branchial arch becomes the dominant respiratory organ (fig. 8C). In *M. albus* the gill filaments are reduced and lack gill rays and typical secondary filaments (fig. 8C). The degenerative trend of the gill filaments culminates in the condition found in *M. boueti,* in which the gill filament becomes a small finger-like

appendage devoid of secondary filaments. However, the highly vascular mucosa has hypertrophied and plays a key role in gas exchange. Concomitant with the reduction of the gill in *M. albus* and *M. boueti,* the buccopharyngeal mucosa becomes folded and highly vascularized, and its epithelium is invaded by numerous intraepithelial capillaries (figs. 8C,F).

In air-breathing Synbranchiformes, exhalation usually precedes inhalation, even though the two actions can be separated in time, since the fish may revert to aquatic breathing after exhaling air (Johansen, 1966). Exhalation in *Monopterus* is always coincident with high activity in the geniohyoideus anterior and posterior, adductor mandibulae, and hyohyoideus superior muscles (fig. 10); by this action, air is expelled from both the mouth and the median external gill slit. As in the less specialized *Synbranchus* (Liem, 1980a), the dominant muscles during exhalation in *Monopterus* are the geniohyoideus posterior and adductor mandibulae A_3 muscles. The combined action of these two muscles generates the compressive force which expels the stale air. This mode of exhalation is independent of water, since the gas bubble is expelled by muscular actions without the aid of water currents. Likewise, inhalation is also accomplished without the use of water. Synchronous high amplitude activity in the hypaxial and sternohyoideus muscles lowers the floor of the buccopharyngeal cavity, thereby creating the low pressure by which air is drawn in through the mouth, which is partially opened by activity in the levator operculi muscle (fig. 11). Thus both exhalation and
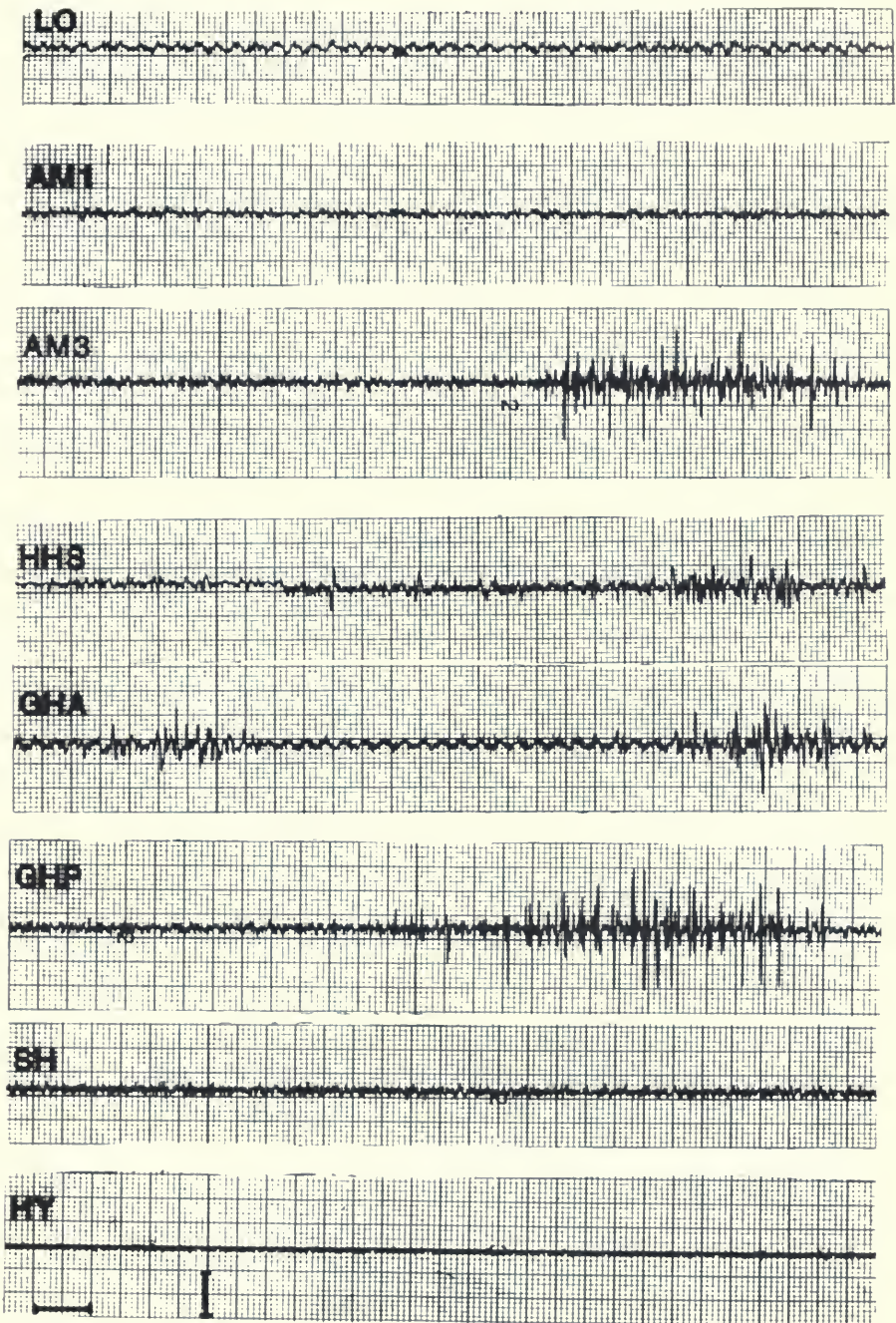
FIG. 10. Representative electromyogram of the principal respiratory muscle of *Monopterus albus* during active exhalation of air. Only four of the eight muscles are active. AM1 = part A_1 of the adductor mandibulae muscle; AM3 = part A_3 of the adductor mandibulae muscle; GHA = geniohyoideus anterior muscle; GHP = geniohyoideus posterior muscle; HHS = hyohyoideus superior muscle; HY = hypaxial muscles; LO = levator operculi muscle; SH = sternohyoideus muscle. Vertical scale is 25 μV; horizontal scale is 50 msec.
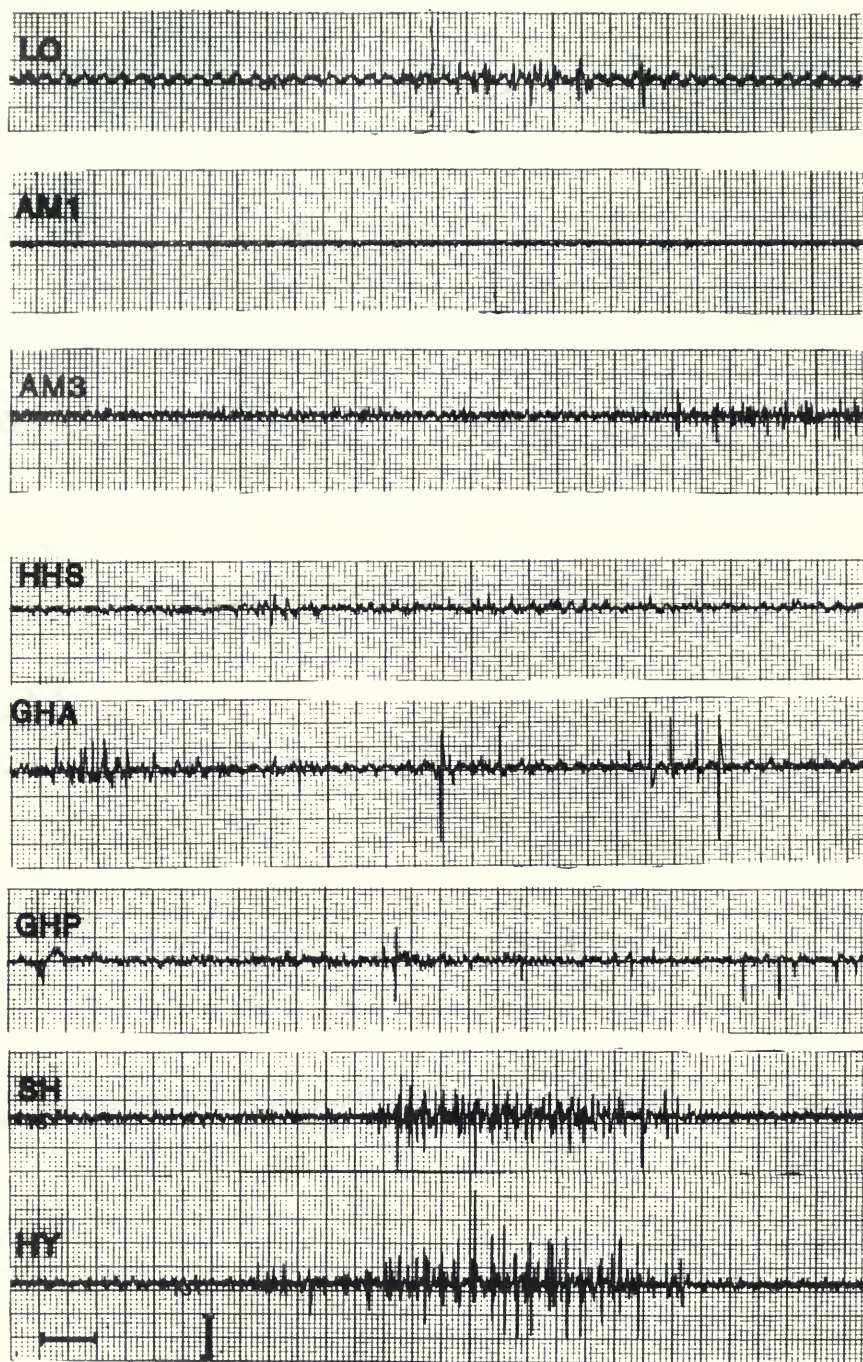
inhalation

FIG. 11. Representative electromyogram of *Monopterus albus* during inhalation of air. See Figure 10 for explanation.
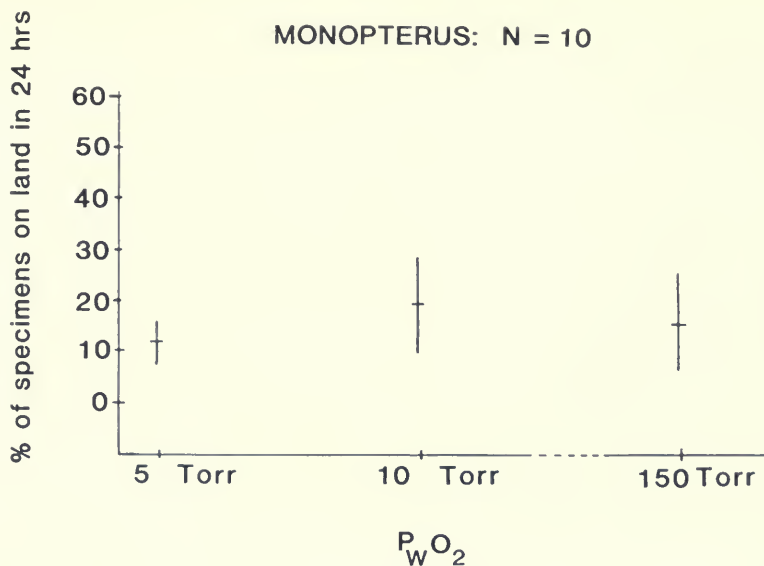
FIG. 12. Frequencies of terrestrial excursions of groups of *Monopterus albus* (N = 10) during 24-hour tests in which fish were exposed to two levels of hypoxia (5 and 10 torr) and to normoxic water.

inhalation in synbranchiforms proceed without the aid of water currents. Because exhalation and inhalation are temporally separated in synbranchiforms, the triphasic pattern is masked. Exhalation is a compressive phase and is essentially a monophasic pattern. Likewise, inhalation is a monophasic extended expansion. Because the respiratory chamber is placed so far anteriorly, the compressive phase has been deleted. Preliminary recordings on *M. cuchia,* which possesses a pharyngeal pouch, show that the compressive phase does occur and fills the chamber at the end of the ventilatory cycle. Thus the pattern in *Monopterus* can be regarded as a modification or variation of the triphasic pattern.

Laboratory Observations
on Triphasic Species

The effects of oxygen depletion on the behavior of *Monopterus albus* and *Anabas testudineus* were analyzed by exposing the fishes to partial concentrations of dissolved oxygen at 5, 10, and 150 torr, respectively, for 24-hour periods after 14 days of acclimation. When both species were exposed to 5 and 10 torr oxygen partial pressures, emergences from the water occurred at the same level as in the control (table 1). It is clear that even the most reduced levels of oxygen in the water do not trigger

terrestrial excursions by either *Monopterus* (fig. 12) or *Anabas.* Similar results on three specimens of *Clarias batrachus* were obtained.

Raised temperatures do not significantly increase the occurrence of terrestrial excursions in either *Monopterus* or *Anabas* (table 1).

Starvation has a dramatic effect on the frequency of emergences in *Monopterus.* When the fishes were kept in well-aerated waters but were not fed for 14 consecutive days, seven to eight of the 10 specimens of *Anabas* and *Monopterus* were found out of water at each half-hour interval of recording during the 24-hour observation period (table 1; fig. 13). Likewise, increased population density had a marked effect on the occurrence of emergences. A doubling of the population density of *Monopterus* will bring the level of terrestrial excursions up to 70% of the total population (table 1), even when the water was well oxygenated and prey items were abundant. A gradual increment in the population density of *Monopterus* was accompanied by a corresponding increase in terrestrial excursions, even if food availability was kept high (fig. 13). When population density was increased while the fish were not fed, the number of emergences increased dramatically (fig. 13), reaching 100% of the population. These experiments clearly indicate that both population density and food availability have pronounced effects on the frequency of emergences. For *Monopterus,* a combination of in-
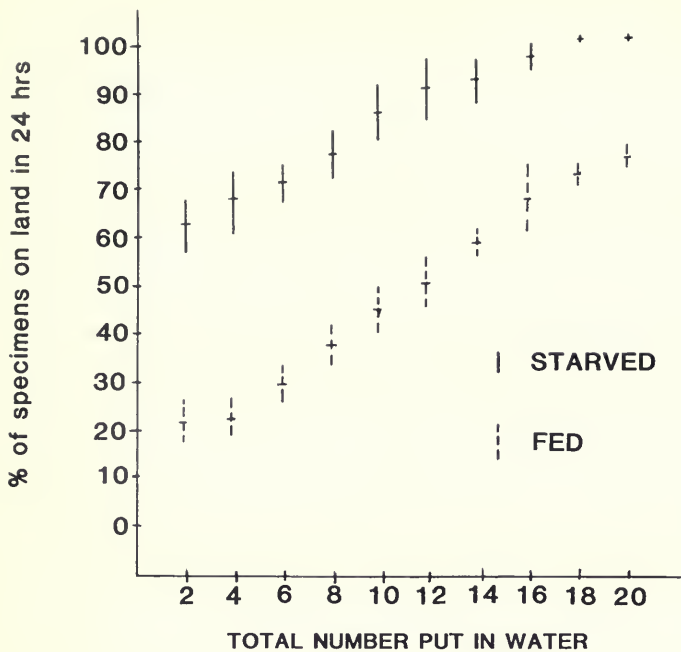
FIG. 13. Frequencies of terrestrial excursions of groups of *Monopterus albus* during 24-hour tests in which fish were subjected to different population densities. One group was composed of well-fed individuals (plotted in broken lines), while the second group consisted of individuals which were starved for 30 days prior to the experiment (plotted in solid line).

creased population density and reduced food resources represents the most powerful trigger for emergence from the water.

Interspecific competition also leads to a higher frequency of emergences by *Monopterus* when it cohabits with the carnivorous species *Nandus nebulosus* (table 1). However, when a population of omnivorous large goldfish (*Carassius auratus*) was added to the *Monopterus* population, it had no significant effect on the behavior of the latter (table 1). Thus interspecific competition acts as a trigger for overland movements by *Monopterus* only when the cohabiting species is feeding on the same prey items; otherwise, interspecific competition does not influence the behavior of *Monopterus*. However, the presence of the aggressive cichlid fish *Oreochromis mossambicus* does have a most profound effect on the terrestrial behavior of *Monopterus* (fig. 14). Even in the presence of only two specimens of *O. mossambicus,* half of the *Monopterus* population (N = 10) emerged from the water within 24 hours. Further additions of *mossambicus* specimens drove almost the entire population of *Monopterus* out of water (fig. 14). When the carnivorous, and thus competitive, but less aggressive *Nandus nandus* was added in gradually increasing numbers to the *Monopterus* population, it caused a proportional and gradual increase in emergences by *Monopterus* (fig. 12). Thus the ag-

onistic behavior received from *O. mossambicus* seems to constitute a more powerful stimulus for *Monopterus* to emerge from the water than does the competition for similar prey by the less aggressive *N. nandus* (fig. 14).

Similar experiments conducted on a population (N = 10) of *Anabas testudineus* have yielded behavioral patterns that closely resemble those of *Monopterus albus*. Starvation resulted in a dramatic increase in the number of terrestrial excursions by *Anabas* (table 1), even when the water was well oxygenated and kept at a constant temperature. A doubling of the population density by adding 10 specimens of *Anabas* invariably increased the frequency of terrestrial excursions, indicating that population pressure triggered emergences from the water (table 1). The addition of 10 goldfish (*Carassius auratus*) had negligible effects on the emerging behavior of the *Anabas* population. The addition of *Nandus, Macropodus,* or *Trichogaster* to the population of *Anabas* resulted in a sharp increase in the frequency of terrestrial excursions by *Anabas*. *Nandus* is a non-air-breathing carnivorous fish which feeds on similar prey items as *Anabas*. Both *Macropodus* and *Trichogaster* are air-breathing fishes, which are moderately aggressive and feed on similar kinds of prey to those of *Anabas*. Lowering of the oxygen concentration in the water to 5 torr did not trigger
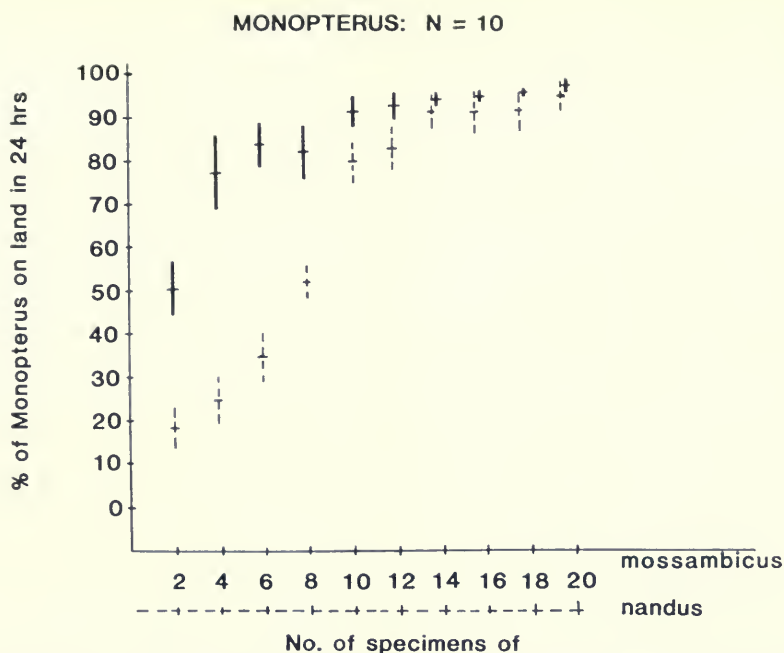
FIG. 14. Frequencies of terrestrial excursions of a group of 10 individuals of *Monopterus albus* during 24-hour tests in which the *Monopterus* population was mixed with an increasing number of individuals of *Oreochromis mossambicus* (plotted in solid lines) and *O. nandus* (plotted in broken lines), respectively.

emergence in *Anabas.* Likewise, a rise in water temperature to 34°C. did not increase the frequency of terrestrial excursions.

Gradual lowering of the water level over a period of 36 hours does not trigger emergence in *Monopterus.* Instead, *Monopterus* will burrow in the sand. *Anabas* retreats in the small puddles of very shallow water in the aquarium before venturing on the elevated sand. Thus, the gradual decrease in water level does not seem to trigger terrestrial excursions in either *Monopterus* or *Anabas.*

**Field Observations
on Triphasic Species**

Numerous field studies have documented that *Anabas testudineus* migrates overland from pond to pond, using its spiny gill-covers as well as its pelvic fins for locomotion (Das, 1927; Munshi, 1968; Dehadrai & Tripathi, 1976). My observations on populations of *Anabas* in various ponds in Western Java confirm that *Anabas* engages in terrestrial excursions. However, such overland excursions from pond to pond are random and occur over wet grassy substrates after rainfall, either at

dawn or dusk. Overland migrations have never been observed during prolonged droughts. When the water levels of the small ponds decrease, the *Anabas* populations remain in the water, even though oxygen levels in the shrinking ponds tend to decrease drastically. Thus, seasonal observations on *Anabas* in ponds in Western Java over a two-year period indicate that terrestrial migrations are restricted to the wet periods, especially after heavy rainfalls. I have never observed any feeding on land by *Anabas.* When ponds shrink, population density increases. Other species inhabiting the ponds are *Monopterus albus, Osphronemus goramy, Helostoma temmincki, Rana chalconota, Rana cancrivora, Bufo* sp., *Cyprinus carpio, Trichogaster trichopterus,* and *Rhacophorus* sp.

I have studied the behavior of *Monopterus albus* in various rice fields, ponds, and streams in and around Bandung (Western Java) over a two-year period. When ponds, rice fields, and streams shrink because of droughts, *M. albus* has never been seen to migrate from drying home waters to larger bodies of water. Instead, the fish retreat to remaining pools and puddles of water and burrow into the mud. When the water becomes very shallow, *M. albus* burrows vertically into the soil. As the water

level continues to fall, *M. albus* burrows deeper and often more obliquely or even horizontally. As a result, the burrow becomes branched and some of the branches remain filled with water even when the pond has completely dried out. Within the burrow the fish continues to be active and can easily be caught by dropping bait into the main burrow. The burrow can be up to 1½ m deep. Thus, the behavior of *M. albus* when prolonged droughts cause bodies of water to shrink or vanish resembles that of the Neotropical *Synbranchus marmoratus* very closely (Lüling, 1980). Neither species aestivates, even during severe prolonged droughts, but remains active in its often elaborate burrow. All individuals of the population of *M. albus* will remain in the water and none will venture on land during the droughts. Likewise, *S. marmoratus* does not engage in overland migrations to escape shrinking bodies of water (Lüling, 1975, 1980). Terrestrial migrations by *M. albus* are restricted to humid days during the wet season and may serve as a mechanism to explore new breeding as well as feeding sites. Numerous migrations can be seen just prior to or during the breeding season. When feeding on land, *M. albus* invariably manipulates its prey by rotating around its long axis (Liem, 1980b). The slightly forward-directed rotational action by the predator and the friction afforded by the substrate against the prey results in the prey being broken and moved into the esophagus. A related species, *Monopterus cuchia,* is also highly amphibious in its behavior (Das, 1927; Munshi & Singh, 1968; Dehadrai & Tripathi, 1976), even though the details of the interactions between environmental parameters and terrestrial excursions are still unknown.

Several species of *Clarias* have been studied in the field (Vaillant, 1895; Smith, 1945; Donnelly, 1973). *Clarias gariepinus* was studied on the Busi River in Zimbabwe (Africa) by Donnelly (1973). Several thousand catfish were stranded in the wet mud of the oxbow formation of the river. Surface flow of the river had ceased, leaving a sandy riverbed. The fish were lying in groups and covered by a film of wet mud. The intake of air by *C. gariepinus* living in the mud was much more frequent (60 per hour) than that of fish living in oxygenated water (12–25 per hour). Air gulping by groups of fish lying in the mud was synchronous. There is no published evidence that *Clarias* leave their aquatic environment during times of drought (Greenwood, 1958, 1961). Upon the refilling of nearly dried-out impoundments, the trapped *Clarias* emerge. In India, Das (1927) has also observed

that *C. batrachus* buries itself in the moist mud 5 or 6 inches below the surface during the dry season. No migrations overland have been observed during the dry season, but with the advent of the monsoon, when the rains begin, *C. batrachus* can often be found out of water. I have observed *C. batrachus* feeding on land in the wet vegetation in Western Java. When feeding on land, *Clarias* grasps its prey and proceeds to rotate about its long axis, wedging the prey against the substrate, thereby pushing the prey back into its pharynx. Such spinning behavior has also been observed by M. N. Bruton (as cited in Helfman & Biggers, 1986) in *C. gariepinus* when feeding on large prey in the water.

Discussion

This analysis of experimental evidence on the mechanisms of air ventilation in fishes explains how specific features in the respiratory apparatus relate to extrinsic environmental factors. In the first part of this discussion I will focus on those results relating to the evolution of structure and function, and then I will attempt to demonstrate the conceptual link between morphology, function, niche utilization, and adaptive radiation.

Structural and Functional Novelties

Air-breathing adaptations have evolved independently in many unrelated lineages of teleosts (Graham, 1976). In this study, members of four phyletically unrelated groups of freshwater fishes are analyzed (fig. 15). The Clariidae are siluroid catfishes belonging to the diverse monophyletic ostariophysan assemblage with a long independent history originating from the basal euteleosts (Fink & Fink, 1981). In sharp contrast, the Channiformes together with the Synbranchiformes represent highly specialized derivatives of the advanced euteleostean Acanthomorpha (Lauder & Liem, 1983). The Anabantoidei (Liem, 1963) do not share a recent common ancestry with either the Clariidae or the Channiformes-Synbranchiformes, but instead have perciform affinities. Strikingly convergent specializations can be found in the four lineages; in each, all or some members develop pharyngeal outpocketings which become air chambers lined with respiratory mucosa (Munshi, 1976). Furthermore, various components of
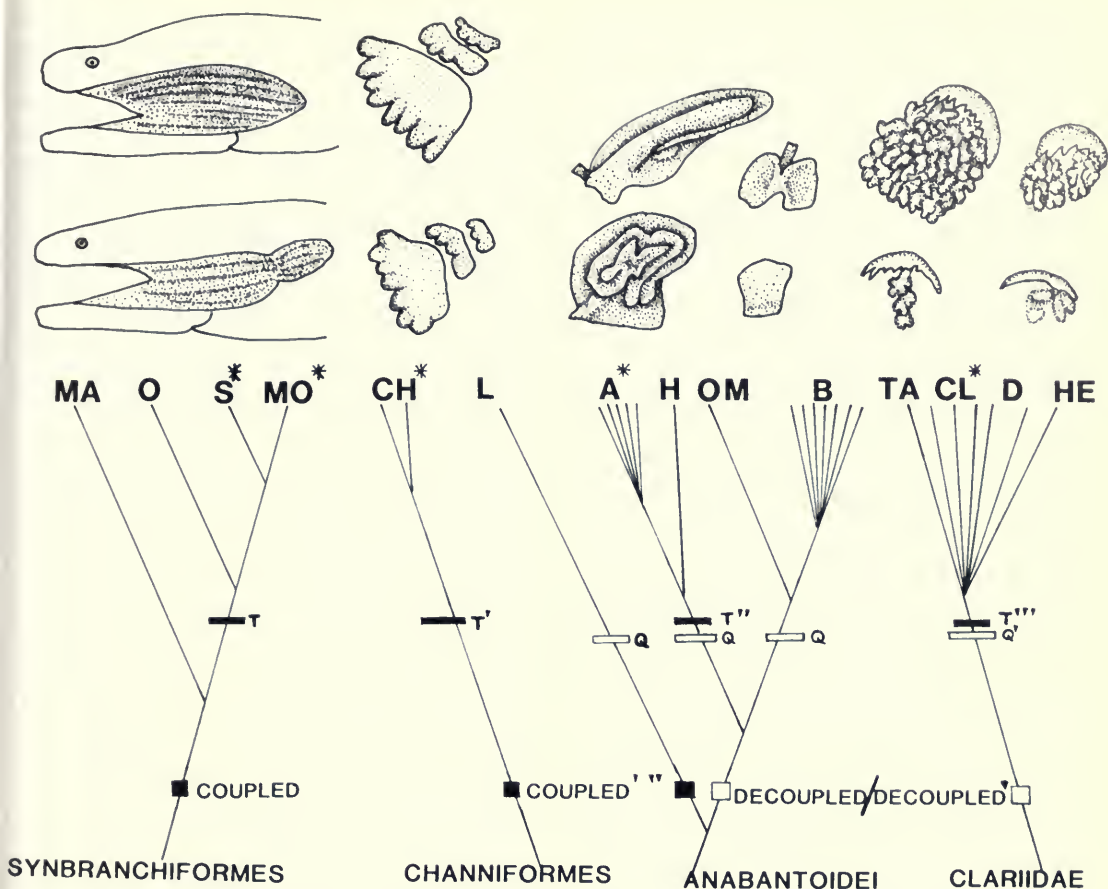
FIG. 15. Four unrelated phyletic lineages of teleost fishes (Rosen & Greenwood, 1976; Lauder & Liem, 1983) in which air breathing has evolved. At top the full variation of the air-breathing elements in each of the four lineages is depicted. Coupled means that feeding or trophic and air chambers are in continuous communication; decoupled means that feeding and air chambers are separated by valves; T, T', T'', and T''' denote triphasic modes of air ventilation; Q and Q' denote quadruphasic modes of air ventilation; * means that the taxon has been recorded to engage in overland movements. A = Anabantidae; B = Belontiidae; CH = *Channa*; CL = *Clarias*; D = *Dinoptopterus*; H = Helostomatidae; HE = *Heterobranchus*; L = Luciocephalidae; MA = *Macrotrema*; MO = *Monopterus*; O = *Ophisternon*; OM = Osphronemidae; S = Synbranchus; and TA = *Tanganikallabes*.

the gill arch elements become either labyrinthic or dendritic, resulting in a great increase in the surface area for gas exchange (fig. 15). Finally, the primary and secondary gill filaments show various degrees of reductive changes (Todd, 1968; Tamura & Moriyama, 1976; Randall et al., 1981). Among air-breathing teleosts the Synbranchiformes are the only monophyletic assemblage in which several closely related species exhibit a complete evolutionary spectrum ranging from purely aquatic forms (*Macrotrema calligans*) to predominantly aquatic bimodal breathers (*Ophisternon aenigmaticum*, *O. bengalense*), balanced bimodal breathers (*Synbranchus* and several species of *Ophisternon*), and, finally, predominantly amphibious species (*Mon-*

opterus cuchia, M. albus, M. boueti, and *M. fossorius*). Thus it is in the Synbranchiformes that the evolutionary pathway for structural changes in relation to bimodal breathing and amphibious life is best preserved.

The gills and associated blood vessels of synbranchids undergo dramatic structural changes as the various species become progressively more amphibious (fig. 8). Four evolutionary novelties are developed within the Synbranchiformes: (1) Extreme modification causes gills to become a narrow flange of tissue; (2) mucosa lining the pharyngeal side of the gill arches becomes highly vascularized; (3) a single affero-efferent vessel is present in the fourth branchial arch (fig. 8C). In *M. cuchia,*

M. fossorius, and *M. boueti,* all four branchial arches each possess a single affero-efferent artery (Rosen & Greenwood, 1976); (4) well-developed suprapharyngeal chambers are present in *M. cuchia, M. fossorius,* and *M. indicus,* but are wanting in *M. albus* and *M. boueti.*

Phylogenetically unrelated groups such as the Clariidae and the Anabantoidei also develop suprabranchial chambers, reductive modifications in the holobranchs, and various shunt vessels between the ventral and dorsal aortae (Satchell, 1976). Synbranchids, clariids, and anabantoids realize closely similar functions in a periodically or chronically deoxygenated aquatic environment. Convergence in the evolution of the respiratory structure-function complex has resulted in the evolutionary development of strikingly similar structural novelties. The independent realization of incipient tendencies in the holobranchs, respiratory mucosa, air chambers, and musculoskeletal features of air-breathing teleosts occurs in parallel in independent lineages. The structural evolution observed in the Synbranchiformes shows in what sequence the specializations are acquired and enables us to recognize the independent development of these rather complex characters in different teleostean lines.

Comparative functional analysis has revealed that the quadruphasic mode of air ventilation has arisen twice during the evolutionary radiations of air-breathing teleosts. It evolved independently in the Anabantoidei and Clariidae (fig. 15, Q, Q'). In both groups the gas bubble is flushed from the suprabranchial chamber by a flow of water. Even though the pattern of exhalation is virtually identical in the two groups, the underlying mechanisms differ, reflecting convergent evolution. In the quadruphasic anabantoids the gas bubble is invariably expelled through the mouth, while in clariids the gas bubbles emerge from under the operculum (Hellin & Chardon, 1983). Within the Anabantoidei, some members of the primitive family Anabantidae and the Helostomatidae breathe triphasically as well as quadruphasically (fig. 15, Q, T"). Unfortunately our knowledge on the Clariidae is still too limited for any generalization. However, *Clarias batrachus* and *C. gariepinus* are capable of breathing either quadruphasically or triphasically, depending on the nature of the environmental conditions. Whether a fish breathes quadruphasically or triphasically cannot be predicted from the morphology of the respiratory apparatus. *Anabas* breathes only triphasically, yet the design of its respiratory system is virtually identical to

that of the quadruphasically breathing *Ctenopoma kingsleyi* (Peters, 1978). Because in quadruphasic ventilation water is used to flush out the gas bubble from the respiratory chamber, exclusively quadruphasic breathers are chained to the aquatic habitat and cannot engage in overland movements. Field studies confirm this prediction derived from laboratory studies: Luciocephalidae, Osphronemidae, and Belontiidae (fig. 15) are never found out of water. This study has shown that rather cryptic functional specializations play a greater role in determining the adaptive zone of air-breathing fishes than the more apparent morphological features.

Triphasic ventilation may well represent the evolutionarily more primitive mode. It is not only widely distributed among the four lineages studied (fig. 15, T, T', T", T'''), but its kinematic, pressure, and electromyographic patterns are very similar in the four lineages (figs. 6–7) even though modifications do occur to accommodate the particular site of the respiratory chamber in *Monopterus* (figs. 4–5, 10–11) and in *Channa* (Liem, 1984). Since triphasic ventilation does not require water, all fishes known to engage in overland movements are triphasic breathers (fig. 15, *).

The specialized quadruphasic mode of air ventilation is an evolutionary novelty which originated from the primitive cough mechanism present in all teleost fishes. This study supports the hypothesis (Liem, 1980a, 1985) that the neuromuscular pattern underlying the original cough mechanism has been shifted into a radically new context: Instead of flushing debris out of the mouth by means of a reversed jet stream of water, the reversed water current serves to eliminate the respiratory gas bubble. This comparative functional analysis has shown that an existing function in conjunction with a new structural design involving simple mechanical water shunts into the air chamber can result in an evolutionary novelty with a dramatic change in function.

Significance of Laboratory and Field Observations

Many scenarios have been built on the physiological and anatomical preadaptations and the supposedly specific environmental conditions which have led to the evolutionary emergence of tetrapods. Yet no attempts have been made to determine the factors triggering emergences from the water by living, air-breathing primitive fishes and teleosts. In this study a series of experiments

were conducted to expose fishes to various environmental perturbations. The results (table 1; fig. 12) suggest that air-breathing fishes remain in water when oxygen or water levels drop. These laboratory findings are confirmed by field studies on the synbranchiform *Synbranchus* (Lüling, 1980), and the clariid *Clarias gariepinus* (Donnelly, 1973). Congruence of the laboratory observations with those obtained in the field enables us to draw a general conclusion that when air-breathing fishes are subjected to hypoxic and drought conditions, they do not engage in terrestrial excursions, but instead remain in water and even dig elaborate burrows in the substrate.

Recent evidence indicates that the evolutionary trajectory of vertebrate species is often determined by occasional bottlenecks of intense selection during a small portion of their history (Wiens, 1977; Boag & Grant, 1981; McKaye & Marsh, 1983; Liem & Kaufman, 1984). A series of experimental procedures were executed to demonstrate the effects of environmental perturbations, which are designed to simulate bottlenecks of intense selection on the emergence behavior of various air-breathing fishes. *Monopterus, Anabas,* and *Clarias* respond by increasing significantly the frequency of emergences from the water when subjected to starvation (fig. 13) or increased intra- and interspecific population density (table 1). If competition is defined as the acquisition of common resources in short supply, my laboratory experiments suggest that competition triggers emergence behavior in *Monopterus* when mixed with a *Nandus* population, while a population of *Anabas* increases its frequency of emergences when mixed with *Nandus, Macropodus,* and *Trichogaster* populations, all of which feed on shared prey items in short supply (table 1).

Unfortunately, the effects of population density and competition on the emergence behavior of air-breathing fishes have never been analyzed in the field. Thus, general conclusions on the causal relationship between overland movements and intra- and interspecific competition of air-breathing fishes await in-depth ecological and behavioral studies. However, one should not *a priori* reject as laboratory artifacts the findings obtained in the laboratory that intra- and interspecific competition represents a powerful trigger for air-breathing fishes to engage in overland movements. Contrary to common belief, there appear to be no papers demonstrating that conclusions concerning behavioral patterns of animals obtained under carefully designed laboratory conditions have been falsified by subsequent field observations. Thus, this study offers a testable hypothesis that some air-breathing fishes respond with overland excursions when subjected to intra- and interspecific competition.

Functional Design and Diversity in Air-Breathing Fish Lineages

In the air-breathing fishes examined, we can decipher extensive interactions between the functionally and anatomically adjacent trophic chamber and the air chambers (figs. 2, 7). Because a change in one feature (e.g., the air-breathing apparatus) may influence the size, shape, and function of an adjacent feature (e.g., the trophic apparatus), a network of interacting constraints results. The network is defined as the relationships of the distinct anatomical elements and the interconnections between the elements (fig. 16). It is hypothesized that the possible pathways for change in design are limited by the nature of the interacting constraints (Liem, 1980b).

Among the four air-breathing fish lineages, we can distinguish two kinds of networks of interacting constraints (fig. 16). The feeding (trophic) chamber and the air chamber can either be coupled or decoupled (figs. 15–16).

In the coupled network of interacting constraints the trophic and respiratory chambers are in continuous open communication with each other. Because of the open connection, changes in pressures in the air chambers follow those of the buccal (feeding) chamber faithfully. As a result, the feeding and air chambers are coupled functionally as well as anatomically. An anatomical change in the air chamber will cause a corresponding change in the trophic chamber and vice-versa because of the close interconnection. Coupled networks are found in all Synbranchiformes, Channiformes, and among the Anabantoidei in the Luciocephalidae (fig. 15).

In the decoupled network, the suprabranchial air chambers become decoupled from the trophic chamber by the development of valves between the various chambers (Munshi, 1962, 1968; Peters, 1978; Liem, 1980a; Hellin & Chardon, 1983; Maina & Maloiy, 1986). As a result, changes in pressures in the buccal (trophic) chamber do not affect those in the air chambers. Thus the trophic and air chambers are decoupled functionally as well as anatomically (fig. 16). Changes in the anatomical configuration of the air chambers and

NATURE OF
NETWORK OF INTER-
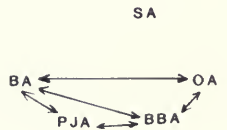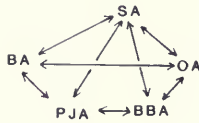ACTING CONSTRAINTS

COUPLED
(NO VALVES)

DECOUPLED
(VALVES)

AIR VENTILATION
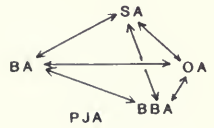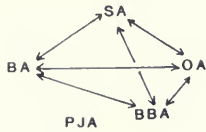
FEEDING

PREDICTIONS:

CONSERVATIVE SA MORPHOLOGY

DIVERSE SA MORPHOLOGY

HISTORICAL TEST:

LUCIOCEPHALIDAE (1G, 1 Sp) ——————— ANABANTOIDEI (15G, 85 Sp)

CHANNIFORMES (1G, 25 Sp)

CLARIIDAE (13G, 100 Sp)

SYNBRANCHIFORMES (4G, 15 Sp)

FIG. 16. Diagram of the networks of interacting constraints of the four lineages depicted in Figure 15. Structural elements of buccal or feeding apparatus (BA), branchial apparatus (BBA), opercular apparatus (OA), pharyngeal jaw apparatus (PJA), and suprabranchial apparatus or air chamber and associated elements (SA) interact by means of their various properties. The activities realized are air ventilation and feeding. The network of interacting constraints is expressed in a diagram in which the relation between the elements is indicated by arrows running between the elements (Liem, 1980b). Since dominance is still undetermined, the arrows are drawn in both directions. In the coupled network, the major elements are interconnected during feeding. In the decoupled network, the suprabranchial apparatus or air chamber and associated elements are dissociated from the other components. The prediction is that the diversity of suprabranchial apparatus morphology (elements associated with the air chamber) will be different, depending on the nature of the network, whether it is coupled or decoupled. Line between Luciocephalidae and Anabantoidei depicts a phyletic relationship; G = genus, Sp = species.

associated elements can occur independently without causing any modifications in the form and function of the trophic chamber, and vice-versa. Decoupled networks of interacting constraints are found in the Anabantoidei (except the Luciocephalidae) and Clariidae.

The results of this study show an inverse correlation between morphological diversity in a lineage and the number of interacting constraints. The hypothesis can be stated as follows: lineages with decoupled air and feeding chambers possess a greater morphological diversity in the elements

associated with the air chamber than lineages in which the chambers are coupled (fig. 16). The hypothesis can be tested by demonstrating repeated independent occurrences of morphological diversity of the air breathing apparatus within lineages possessing decoupled networks of interacting constraints. The results of the tests are summarized in Figures 15 and 16. It is clear that morphological diversity of the labyrinthic and dendritic organs in the Clariidae and Anabantoidei is correlated with the decoupled pattern (fig. 15). Furthermore, the reverse of the predicted effects of decoupling

can also be demonstrated: Coupling of the feeding and air chambers correlate with reduced morphological diversity of the air-breathing elements in the Synbranchiformes and Channiformes (fig. 15). Thus, morphological diversity in the design of the elements involved in air-breathing functions is largely determined by the nature (coupled versus decoupled) of the network of interacting constraints rather than by selective forces of environmental (extrinsic) factors. Members of the four lineages often inhabit the same microhabitats in ponds in Java, Kalimantan, and Sumatra (Vaas, 1952; Vaas et al., 1953; Inger, 1955; Dehadrai & Tripathi, 1976; pers. obs.). Thus, current evidence indicates extensive ecological overlap and sympatry of the Channiformes, some members of the Synbranchiformes, the Anabantoidei, and the Clariidae.

It is probable that very similar extrinsic selection forces have acted on the air-breathing organs of the four sympatric lineages during much of their evolutionary history. The very different evolutionary products (diverse versus conservative air-breathing organ morphology) can therefore be explained on the basis of the differences in the nature of the network of interacting constraints (coupled versus decoupled) rather than on the basis of different extrinsic selective forces acting on the air-breathing apparatus. Even though decoupling of a previously coupled or constrained system may not necessarily lead to higher taxonomic diversity (Lauder, 1981), this comparative analysis clearly indicates a substantially higher number of species in the Anabantoidei and Clariidae, both of which have decoupled systems, while the lineages with coupled systems (Synbranchiformes, Channiformes, and Luciocephalidae) have a much lower taxonomic diversity (fig. 16).

The Meaning of Overland Movements

Graham (1973, 1976) has contrasted the overland movements in air-breathing freshwater and marine fishes. The majority of marine air-breathing fishes are amphibious, and air breathing is continuous, with rapid and complete transitions between aerial and aquatic respiration. Amphibious marine fish engage in terrestrial sojourns to avoid competition and to exploit successfully habitats that are not saturated with competitors and predators (Sponder & Lauder, 1981). In contrast, most freshwater air-breathers are not amphibious and breathe air in response to seasonally recurring conditions of stagnation and hypoxia (Graham, 1976). This study on freshwater air-breathing fishes has established that only triphasically breathing species are preadapted for the invasion of terrestrial habitats and that quadruphasic species are totally dependent on water in order to breathe air. However, laboratory experiments have shown that all freshwater air-breathing fishes remain in water when oxygen concentrations decrease (table 1; fig. 10), temperatures increase (table 1), or water levels fall (Lüling, 1980; Johnels, 1957; Donnelly, 1973). Smaller bodies of water in the tropics are periodically deficient in oxygen and only fishes capable of utilizing atmospheric oxygen thrive in them. As Inger (1957) suggested, the abundance of air-breathing fishes in these warm, stagnant waters is indicative that the original selective advantage of air breathing was to enable fishes to *remain* in the water. During prolonged dry seasons, *Anabas* (Smith, 1945), *Channa* (Smith, 1945), *Synbranchus marmoratus* (Lüling, 1980), *Monopterus cuchia* (Das, 1940; Munshi & Singh, 1968), *M. albus* (Liem, 1967b), *Clarias* (Vaillant, 1895; Smith, 1945; Greenwood, 1958; Donnelly, 1973), and *Heteropneustes* (Smith, 1945) either burrow or otherwise remain in the mud, and none is reported to migrate from drying pools to larger bodies of water. Migrations over land only occur after heavy rains when the substrate is moist. An effective mechanism of air ventilation that does not use water as the flushing force permits the fish to engage in overland movements. Such terrestrial excursions facilitate the invasion of new aquatic habitats to reduce competition in heavily populated waters, the exploitation of new "pioneer" terrestrial habitats, and a wider dispersal. The experimental evidence obtained under controlled laboratory conditions (table 1; figs. 12–13) and the congruent data from field studies (Smith, 1945; Greenwood, 1958; Lüling, 1975, 1980; Donnelly, 1973; pers. obs. in Western Java) lend strong support for Inger's theory (1957) that the proximate selective factor in the first terrestrial activities of the prototetrapods may well have been population pressure in a continuously humid climate. The alternative widely accepted hypothesis, that when streams or pools dried up at the close of the Devonian (Romer & Parsons, 1977, p. 63) the prototetrapods were crawling up or down the stream bed in search of some surviving bodies of water, must be rejected in the absence of any supporting biological evidence.

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